52 Family Gyliauchenidae Fukui, 1929

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Introduction

The Gyliauchenidae Fukui, 1929 comprises approximately 30 species, which are almost entirely restricted to herbivorous teleost fishes in the Indo-West Pacific. The family occurs predominantly in fishes of, in descending order of importance, the Siganidae, Acanthuridae, Scaridae, Pomacanthidae, Chaetodontidae and Zanclidae. These families account for over 80% of the reports of the Gyliauchenidae. This host restriction is correlated with a suite of morphological adaptations that define the group. Gyliauchenids are characterized principally by specialization of the digestive system. The oral sucker has been lost and functionally replaced by the pharynx. In some species, the oesophagus is long and convoluted, forming many coils within the forebody, and the pharynx has been functionally replaced by the oesophageal bulb, which is formed from increased posterior muscularization of the oesophageal wall. Most gyliauchenids are further adapted to the host environment of herbivory by the possession of a posterior ventral sucker. The complexity of the structure of the oesophagus of gyliauchenids, coupled with the paucity of other morphological features, has confounded their taxonomy. They have been associated with a number of digenean groups, including the Paramphistomoidea Fischoeder, 1901, with which they share superficial similarity. Nahhas & Wetzel (1995) conducted the most recent review of the group, but did not recognize the phylogenetically important and morphologically uncharacteristic genus *Petalocotyle* Ozaki, 1934, nor consider the striking similarities between gyliauchenids and the enigmatic *Robphildollfusium* Paggi & Orecchia, 1963.

The first record of a gyliauchenid was the description of *Gyliauchen tarachodes* Nicoll, 1915 from the intestine of a 'pilot fish', *Tachysurus* sp. (Ariidae), from north Queensland, Australia (Nicoll, 1915). Nicoll placed *Gyliauchen* Nicoll, 1915 in the Paramphistomatidae [*sic*] Fischoeder, 1901 but could not classify it within a subfamily. He acknowledged that *Gyliauchen*, with its unusual convoluted oesophagus, was aberrant for the family, but believed that it was sufficiently similar to include it there. The specific identity of the type-host for *G. tarachodes* appears unlikely to be resolved. Nicoll (1915) stated that the species of *Tachysurus* was unknown and was, in his opinion, a new species ('*Tachysurus* n. sp.'). *Tachysurus* is in the marine catfish family Ariidae and, as far as we

are aware, ariids have never otherwise been reported as hosts of gyliauchenids and are never referred to as 'pilot fish'. Further, ariids are not herbivorous and, given the host-range of other gyliauchenids, are unlikely to harbour this family. *G. tarachodes* has never since been collected.

Shortly after the proposal of *Gyliauchen*, Goto & Matsudaira (1918) erected *Dissotrema* Goto & Matsudaira, 1918 for *D. papillatum* Goto & Matsudaira, 1918, from the intestine of *Siganus fuscescens* from Japanese waters. Although they recognized the superficial similarity between *Dissotrema* and other taxa with posterior ventral suckers, Goto & Matsudaira believed that differences in the topography of the gonads and the nature of the vitellarium warranted a new family, the Dissotrematidae Goto & Matsudaira, 1918, which they diagnosed by the posterior ventral sucker, the long, convoluted oesophagus with a proximal oesophageal bulb, the pretesticular ovary and the absence of pharyngeal sacs. The following year, Goto (1919) synonymized *Dissotrema* with *Gyliauchen*, concluding that a distinct family was still justified for *Gyliauchen* but without providing a name for the group. It was not until a decade later that the family-group name Gyliaucheninae was first used by Fukui (1929), who revised the amphistomatous digeneans and proposed the Opistholebetidae Fukui, 1929 and two subfamilies, the Opistholebetinae Fukui, 1929 and the Gyliaucheninae Fukui, 1929. The Gyliaucheninae included only *Gyliauchen*, which was recognized as the senior synonym of *Dissotrema*. Fukui made no comment on the prior proposal of the Dissotrematidae, although he referred to both the relevant papers. Shortly after, Ozaki (1933) described a new genus and species, *Telotrema caudatum* Ozaki, 1933 in the 'Gyliauchenidae (Goto & Matsudaira)'. In his discussion, Ozaki mentioned the synonymy of *Dissotrema* with *Gyliauchen* and appeared to attempt to reflect this in the form of authority he used in the title of the paper. Subsequently, Ozaki cited the group as the 'Gyliauchenidae Ozaki, 1933' (e.g. Ozaki, 1936b, 1937a, b). Successive usage has largely adopted 'Ozaki, 1933' as the authority for the family although 'Goto & Matsudaira, 1918' has also been used (e.g. Hall & Chambers, 1999; Hall & Cribb, 2000). We argue that the citation, according to recommendations of the International Code of Zoological Nomenclature (Articles 36.1 and 40.2), is best as Gyliauchenidae Fukui, 1929.

The most important work on the family was the series of studies by Ozaki (1933, 1934a, b, 1936b, 1937a, b), in which he proposed the new genera *Telotrema* Ozaki, 1933, *Petalocotyle* and *Flagellotrema* Ozaki, 1936, described five new species and recognized the group at the family level, independent of the Opistholebetidae. Further new genera were proposed by Yamaguti (1934, 1942), Caballero y Caballero & Bravo-Hollis (1952), Manter & Pritchard (1962), Shalaby & Hassanine (1997a) and Hall & Chambers (1999). The family has been formally reviewed twice (Ozaki, 1937a, b; Nahhas & Wetzel, 1995) and, although the composition of the family has changed through the addition and subtraction of various genera, the diagnosis of the family has remained comparable to that initially proposed by Goto & Matsudaira (1918) for the Dissotrematidae.

The family displays remarkable and varying specialization that relates to the herbivorous diet of both the definitive hosts and the gyliauchenids themselves. The most important features are the forms of the attachment organs and the gut. In all genera except *Petalocotyle* and *Robphildollfusium*, the ventral sucker is either at or close to the posterior end of the body. Anatomically, the posterior end of the body is probably actually the point at which the excretory pore opens, but this often occupies an apparently anterodorsal position. It is likely this position is achieved by the kind of ontogenetic change that Cable (1954c) described for the Opistholebetidae, which also often have a posterior ventral sucker, but this has not been demonstrated. Frequently, the excretory pore opens on a distinct protuberance called the excretory papilla.

Gyliauchenids possess only a single muscular structure at the anterior end, about which there has been much debate. Early workers regarded this organ as an oral sucker and the organ immediately anterior to the intestinal bifurcation as a pharynx. Ozaki (1937b) examined the histology of the 'pharynx' and determined that it was derived from oesophageal cells and was not a separate, membrane-bound structure. It has strongly developed longitudinal and circular muscle fibres and is best referred to as the oesophageal bulb. Significant muscularization of the oesophagus along its entire length is not observed; in gyliauchenids, muscularization of the oesophagus appears to be restricted to the proximal portion, immediately anterior to the intestinal bifurcation. It remains uncertain whether the anterior-most organ is an oral sucker or a pharynx. The near dorsoventral symmetry of the structure led Pearson (1992) and Hall & Cribb (2000) to consider it a pharynx. This interpretation is accepted here but it is acknowledged that this is not accepted universally.

The gut of all gyliauchenids is specialized in comparison to that of the phylogenetically closest group, the Lepocreadiidae Nicoll, 1914. The degree of specialization of the oesophagus and caeca differs among the genera. The species of *Petalocotyle* display the simplest configuration. The oesophagus is relatively short and straight and, although it is surrounded by gland-cells, they are comparatively scant and the wall of the oesophagus is thin. The oesophageal bulb is small and poorly developed in this group. The caeca are long, reaching the posterior extremity, and the gastrodermis is simple and thin. In species of *Paragyliauchen* Yamaguti, 1934, *Leptobulbus* Manter & Pritchard, 1962 and *Apharyngogyliauchen* Yamaguti, 1942, the caeca are still long, but shorter than in *Petalocotyle*, and they have a thicker gastrodermis; in some species, they are almost compartmentalized, with septa-like divisions that appear to partition the caeca. The oesophageal bulb of species of *Leptobulbus* is less developed than in species of *Paragyliauchen*. In contrast to *Leptobulbus* and *Paragyliauchen*, species of *Apharyngogyliauchen* have no oesophageal bulb. The most specialized and complex arrangement is seen in species of *Gyliauchen* (see Jones *et al.*, 2000). In these (most notably *G. nahaensis* Ozaki, 1937 and *G. parapapillatus* Nahhas & Wetzel, 1995), the oesophagus is remarkably elongate and coiled in the forebody, reaching lengths greater than the overall length of the worm, has a thick lining and is associated with dense glands. The oesophageal bulb is large and well developed and the caeca are short (less than a third of the body-length) with a thickened gastrodermis.

The reproductive system of gyliauchenids is unexceptional except in the male terminal genitalia. The male system always consists of two testes, which lead to a remarkable cirrus-sac, described by Ozaki (1937b). The terminal genital ducts consist of a large tubular, often bipartite, seminal vesicle that is partly external to the cirrus-sac. This opens into a large, prominent internal pars prostatica. The pars prostatica is fed by profuse glands, external to the cirrus-sac, which pass through fixed openings in the wall of the cirrus-sac. This morphology is here interpreted as a synapomorphy for the Gyliauchenidae. In addition, there is a well-developed eversible ejaculatory duct and large everted cirri are observed frequently. In some species, the ejaculatory duct is long and convoluted (especially in *Petalocotyle* spp.) and in others it is ornate and lined with anucleate papilla-like bodies. The female system comprises an ovary, extensive vitelline follicles, Laurer's canal, canalicular seminal receptacle and a uterus that winds between the ovary and the genital pore. The egg-forming complex is distinguished by the presence of an insemination chamber between the ovary and the oötype. This chamber is a small swelling of the oviduct, which is fed directly by the ovary and seminal receptacle and is, presumably, the site of fertilization; zygotes pass from the chamber to the oötype via the short oviduct. Tanned, operculate eggs are produced. The genital pore is always median and approximately half-way

between the pharynx and the ventral sucker and is sometimes embellished with musculature, a cilia-like lining or gland-cells.

The unusual morphology of the gyliauchenids has led to long speculation about their phylogenetic relationships. The two established hypotheses of their affinities – that they are related to paramphistomoids and that they are aberrant lepocreadiids (Pearson, 1992) – have been tested with molecular data (Barker *et al*., 1993b; Blair & Barker, 1993), which indicated a monophyletic assemblage comprising the Lepocreadiidae, Enenteridae Yamaguti, 1958 and Gyliauchenidae. This was supported by the molecular analyses of Cribb *et al*. (2001) and Olson *et al*. (2003). A phylogenetic relationship with the Lepocreadiidae suggests that the oral sucker has been lost in the Gyliauchenidae, that the posterior position of the ventral sucker is apomorphic within the group and that its position in *Petalocotyle* represents the plesiomorphic condition.

A problematic genus sometimes associated with the Gyliauchenidae is *Robphildollfusium* Paggi & Orecchia, 1963, erected for *Distomum fractum* Rudolphi, 1819 within a new monotypic family, the Robphildollfusiidae Paggi & Orecchia, 1963, by Paggi & Orecchia (1963). Goto (1919) first suggested the possibility of an association between *Gyliauchen* and *R. fractum* (Rudolphi, 1819), based on similarities of the male terminal genitalia. There are many parallels between *Robphildollfusium* and other gyliauchenids, especially with *Petalocotyle*, which suggest that the continued recognition of the Robphildollfusiidae Paggi & Orecchia, 1963 is not valid. *Robphildollfusium* has never formally been included within the Gyliauchenidae, although Yamaguti (1971) united *Robphildollfusium* and *Petalocotyle* in the Petalocotylinae Ozaki, 1937, as a subfamily of the Lepocreadiidae. The view taken here is that *Robphildollfusium* is remarkably similar to, yet distinct from *Petalocotyle*. The morphological similarities between species of *Petalocotyle* and *Robphildollfusium* are supported by recent DNA sequence data (Peter Olson, personal communication), which indicate that the phylogenetic position of *Robphildollfusium* is basal within the Gyliauchenidae (unpublished data). Thus, the Robphildollfusiidae is here recognized as a junior synonym of the Gyliauchenidae and *Robphildollfusium* is placed in the subfamily Robphildollfusiinae Paggi & Orecchia, 1963, which is diagnosed principally by the anterior position of the ventral sucker and the presence of separate male and female genital pores.

Nothing is known of the gyliauchenid life-cycle and this remains a conspicuous gap in the knowledge of this family. A phylogenetic relationship with the Lepocreadiidae suggests that the first intermediate hosts are likely to be gastropods. The concentration of the family in herbivorous fishes suggests that the life-cycle might incorporate a cercaria that encysts on algae, as has been shown for the Haploporidae Nicoll, 1914 and Haplosplanchnidae Poche, 1926, but the possibility that there is a second intermediate host that lives among algae cannot be discounted.

Classification

There have been few attempts to investigate the intergeneric relationships of the Gyliauchenidae. Five subfamilies have been proposed: the Gyliaucheninae, Apharyngogyliaucheninae Yamaguti, 1942, Ichthyotreminae Caballero & Bravo-Hollis, 1953, Petalocotylinae Ozaki, 1937 and the Robphildollfusiinae. Three, the Gyliaucheninae, Petalocotylinae and Robphildollfusiinae, are recognized here. The Petalocotylinae contains only *Petalocotyle*, which is the least distinctive of the gyliauchenids in that its ventral sucker is in the typical position for digeneans, towards the anterior end of the body. The Robphildollfusiinae contains only *Robphildollfusium* and is characterized by the position of the ventral sucker in the anterior half of the body and the possession

of separate male and female genital pores. All remaining genera have the ventral sucker at or close to the posterior end of the body and are here classified within the Gyliaucheninae, which is diagnosed by that character; we see no value in the recognition of monotypic subfamilies for *Apharyngogyliauchen* and *Ichthyotrema* Caballero & Bravo-Hollis, 1953.

Ten genera have been proposed that agree with our concept of the Gyliaucheninae. Of these, only *Dissotrema* and *Telotrema* are not presently recognized. *Dissotrema* was synonymized with *Gyliauchen* almost immediately subsequent to its proposal. *Telotrema* was also synonymized with *Gyliauchen* by Yamaguti (1934); this synonymy has been largely maintained in the literature, but the genus was recognized by Winter (1960) and is also recognized here. Of the genera we recognize, *Affecauda*, *Apharyngogyliauchen* and *Ichthyotrema* are each unambiguously distinguished in the key below. The other genera, including one new genus, differ from each other in the combination of the degree of development and position of the oesophageal bulb, the ventral sucker, the oesophagus and the ovary. We have considered each of these genera and all their constituent species and comment below.

Genera *Gyliauchen* Nicoll, 1915 and *Progyliauchen* Shalaby & Hassanine, 1997

Gyliauchen, the type- and largest genus, currently includes 11 species. Seven of the species are reported partly or entirely from siganids and, although another nine families of fishes are reported as hosts, only the closely related and monotypic Zanclidae is reported to harbour more than one species (two). The genus has clearly radiated within the Siganidae and individual fishes frequently harbour hundreds of individuals of several species. Of those species not reported from siganids, we have argued above that the ariid host of the type-species is not credible and we conclude that it was likely to have been a siganid. The lack of an oesophageal bulb in *G. thalassame* Wang, 1977 indicates clearly that it belongs in *Apharyngogyliauchen*, to which it is here transferred as *A. thalassame* (Wang, 1977) n. comb. *G. pomacentri* Nahhas & Wetzel, 1995 is conspicuous in the genus in lacking a convoluted oesophagus and having a pharynx that is relatively enormous compared to the oesophageal bulb. The species was described from only a single, damaged specimen and bears considerable resemblance to *Telotrema*; this similarity was acknowledged by Nahhas & Wetzel (1995) and, certainly, it does not agree with our concept of *Gyliauchen*. We here transfer it to *Telotrema* as *T. pomacentri* (Nahhas & Wetzel, 1995) n. comb. In the light of these conclusions, only one species, *G. indicum* Gupta & Tandon, 1983 (from a clupeid), has an unchallenged host-range not reported to include a siganid or zanclid, and this record is unconfirmed.

Gyliauchen is recognized for the combination of the ventral sucker at or close to the posterior end of the body, a convoluted oesophagus that forms at least one loop and reaches lengths (when straightened) greater than 50% of the total body-length; in some species, such as *G. nahaensis* Ozaki, 1937, the oesophagus forms multiple loops and is very long, exceeding the length of the body. In addition, species of *Gyliauchen* possess an unlobed ovary, which is anterior to the testes. The only other genus with an oesophagus as long and coiled as in species of *Gyliauchen* is *Progyliauchen* Shalaby & Hassanine, 1997. Its single species, *P. sigani* Shalaby & Hassanine, 1997, was also reported from a siganid and is the only other genus of gyliauchenids reported from siganids. The shared host-group and highly convoluted oesophagus are strong evidence of a close relationship. The only significant distinction between these two genera is that *P. sigani* is reported to have a four-lobed ovary, although in addition the ventral sucker of *P. sigani*

is more distant from the posterior end of the body than in any currently recognized species of *Gyliauchen*. In our view, these differences justify the recognition of *Progyliauchen* as a separate genus, despite its clear relationship to *Gyliauchen*.

The concept of *Gyliauchen* presented here encompasses a great deal of morphological complexity, particularly with respect to the structure of the oesophagus. Results from morphological and molecular studies presently in progress indicate that the genus is in need of comprehensive revision. We are currently working on a subdivision of *Gyliauchen*, which will recognize several new genera, and future publications will significantly restrict the concept of this genus.

Genera *Flagellotrema* Ozaki, 1936 and *Hadrobolbus* n. g.

There are presently four species in *Flagellotrema*. Like *Gyliauchen*, species of *Flagellotrema* have a convoluted oesophagus, although its length relative to the total body-length is never greater than 50% of the body-length. In addition, *Flagellotrema* is distinguished from *Gyliauchen* by the position of the ovary which, in its type-species, is intertesticular. The four species of *Flagellotrema* do not form a convincing group. *F. convolutum* Ozaki, 1936, the type-species, is known only from the acanthurid genus *Prionurus* off Japan; it has an elongate body, nearly tandem testes, and the excretory pore is dorso-subterminal on a distinct excretory papilla. The other three species, *F. centropygis* Yamaguti, 1970, *F. chaetodontis* (Manter & Pritchard, 1962) and *F. potteri* Yamaguti, 1970, are all known only from fishes off Hawaii. *F. chaetodontis* has been recorded only from chaetodontid fishes, whereas both *F. centropygis* and *F. potteri* are known from *Centropyge potteri* (Pomacanthidae); *F. potteri* has also been recorded from *Acanthurus triostegus* (Acanthuridae). These three species of *Flagellotrema* are distinctive in having a subterminal ventral sucker, a large oesophageal bulb, diagonal testes and a terminal excretory pore with only a small, inconspicuous excretory papilla. We propose a new genus, *Hadrobolbus*, for these species, with *H. chaetodontis* (Manter & Pritchard, 1962) n. comb. as the type-species, and the new combinations *H. centropygis* (Yamaguti, 1970) n. comb. and *H. potteri* (Yamaguti, 1970) n. comb. Etymology: this genus is named for the massive size of the oesophageal bulb, which is larger than the pharynx. *hadros* (Gk) = well developed, stout, strong; *bolbos* (Gk) = a swelling, bulb.

Genus *Leptobulbus* Manter & Pritchard, 1962

Leptobulbus Manter & Pritchard, 1962 contains only a single species, *L. magnacirratus* Manter & Pritchard, 1962, reported from scarids from Hawaii (Manter & Pritchard, 1962; Yamaguti, 1970). The figure provided by Yamaguti (1970) shows significant differences from the original description and it is possible that his description incorporates additional species. *Leptobulbus* is similar to *Apharyngogyliauchen* in body-shape, but is distinguished from other genera by having, uniquely, a weakly developed oesophageal bulb. Whereas most genera have bulbs that superficially resemble a pharynx, the musculature of the bulb of *Leptobulbus* appears loose and weak. *L. magnacirratus* also has the gonads mainly posterior to the ventral sucker, which is distinctly separate from the posterior extremity.

Genus *Paragyliauchen* Yamaguti, 1934

Paragyliauchen presently has two species, *P. chaetodontis* Yamaguti, 1934 and *P. arusettae* Machida, 1984. It is characterized by its well-developed oesophageal bulb, almost straight or sigmoid oesophagus and ventral sucker well separated from the posterior extremity. *P. chaetodontis* was described by Yamaguti (1934) from a '*Chaetodon* sp.' and was subsequently reported by Ozaki (1937b) from a pomacanthid, *Chaetodontoplus septentrionalis*. We have seen similar species in a second pomacanthid, *Centropyge bispinosus*, on the Great Barrier Reef, but in none of several hundred chaetodontids from several sites in the Indo-Pacific. We think it is likely that the original '*Chaetodon* sp.' was a misidentified pomacanthid. There is an additional dubious host record of *P. chaetodontis* from *Plagiotrema tapeinosoma* (Blenniidae) in Japanese waters (Dyer *et al*., 1988). We have examined this specimen and found that, although immature, it agrees well with *Paragyliauchen chaetodontis*; the immaturity of the specimen makes this record from a carnivorous host seem less credible.

Genus *Telotrema* Ozaki, 1933

Telotrema Ozaki, 1933 is recognized here as valid. It was described for a single species, *T. caudatum* Ozaki, 1933, from the intestine of *Prionurus scalprus* from Japanese waters (Ozaki, 1933). The species is distinguished by a distinctively elongate ventral sucker, a nearly straight oesophagus, an enormous excretory papilla, into which the elongate posterior testis may extend, and the ovary anterior to the ventral sucker. The genus was apparently first synonymized with *Gyliauchen* by Yamaguti (1954), although retained by Winter (1960). Yamaguti (1971) argued that the position of the testes in relation to the ventral sucker is related to the handling of the specimens. Photographs of evidently well-fixed specimens (Ozaki, 1937b) suggest that the extent to which the posterior testis enters the excretory papilla does indeed vary, but the combination of characters exhibited by *T. caudatum* is sufficiently distinct to warrant recognition of the genus.

Family Gyliauchenidae Fukui, 1929[1]

(Syns Dissotrematidae Goto & Matsudaira, 1918; Robphildollfusiidae Paggi & Orecchia, 1963)

Diagnosis: Body elongate to pyriform, up to 5 mm in length. Tegument unarmed. Oral sucker absent. Ventral sucker usually in posterior half of body, frequently at posterior extremity, rarely in anterior half of body (*Petalocotyle* and *Robphildollfusium* spp.). Prepharynx absent. Pharynx surrounds mouth. Oesophagus always well developed, sometimes almost straight, often highly convoluted, surrounded by well-developed gland-cells. Oesophageal bulb usually present, may resemble well-developed pharynx or be less well developed. Intestinal bifurcation generally in anterior third of body. Caeca blind, may extend close to posterior extremity or terminate distinctly short of it, especially when ventral sucker is terminal or nearly so. Testes two, tandem,

[1]Article 40.2 of the International Code of Zoological Nomenclature indicates Gyliauchenidae is the valid family name because, although it is more recent than Dissotrematidae, it is based on the senior synonym of *Dissotrema* and the usage of the more recent name became the prevailing usage prior to 1961.

oblique or symmetrical, globular, in posterior third of body. Seminal vesicle large, tubular, often bipartite, partly external to cirrus-sac, opens into prominent pars prostatica within cirrus-sac. Prostatic gland-cells profuse, external to cirrus-sac; ducts pass through fixed openings in cirrus-sac wall. Cirrus-sac well developed, enclosing pars prostatica and well-developed eversible ejaculatory duct; ejaculatory duct variable in length, sometimes convoluted, ornate or lined with anucleate papilla-like bodies; everted cirrus observed frequently. Genital pore generally median, equatorial. Genital atrium prominent. Ovary entire or less commonly 3–4-lobed, may be between, anterior to, or posterior to, testes. Mehlis' gland well developed. Canalicular seminal receptacle present, associated with insemination chamber. Laurer's canal present. Uterus passes anteriorly from ovary in coils. Metraterm rarely developed. Eggs yellow, operculate, 50–80 μm long. Vitellarium follicular; follicles profuse, may fill hindbody (*Petalocotyle* and *Robphildollfusium* spp.) or, when ventral sucker is close to posterior end of body, more restricted in forebody. Excretory vesicle I-shaped; pore terminal or distinctly dorso-subterminal, often on distinct excretory papilla. Lymphatic ducts present. In intestine of marine teleosts (predominantly herbivorous Siganidae, Acanthuridae, Scaridae, Pomacanthidae, Chaetodontidae, Sparidae and Zanclidae); Indo-Pacific and Atlantic. Type-genus *Gyliauchen* Nicoll, 1915.

Key to subfamilies

1a. Ventral sucker in posterior third of body; vitelline follicles restricted, extend from oesophageal bulb to level of gonads, never reach posterior extremity .... Gyliaucheninae Fukui, 1929.

1b. Ventral sucker in anterior third of body; vitelline follicles extensive, extend from at least level of intestinal bifurcation to posterior extremity ..... 2.

2a. Genital pore common, may be glandular, but without cuticular lamellae; male and female genital atria distinct, but definitely unite anterior to genital pore .... Petalocotylinae Ozaki, 1937.

2b. Male and female genital pores separate; female pore and atria ornamented with cuticular lamellae ..... Robphildollfusiinae Paggi & Orecchia, 1963.

Subfamily Gyliaucheninae Fukui, 1929

(Syns Apharyngogyliaucheninae Yamaguti, 1942; Ichthyotreminae Caballero & Bravo-Hollis, 1953)

Diagnosis: Ventral sucker in posterior half of body, sometimes at posterior extremity. Oesophageal bulb present or absent. Caeca always terminate distinctly short of posterior extremity. Testes two, tandem, oblique or symmetrical, in posterior third of body. Eversible ejaculatory duct short. Ovary entire or, rarely, 3–4-lobed, between, anterior to, or posterior to, testes. Vitelline follicles profuse, generally restricted to mid-body, not reaching posterior extremity. Excretory vesicle short, I-shaped; pore dorso-subterminal; excretory papilla often distinct. Type-genus *Gyliauchen* Nicoll, 1915.

Key to genera

1a. Ovary distinctly posterior to, and separate from, testes; body highly elongate, fusiform ..... *Ichthyotrema* Caballero & Bravo-Hollis, 1952. (Fig. 52.1)

Diagnosis: Body elongate. Ventral sucker close to posterior extremity. Oesophagus relatively straight, not convoluted. Oesophageal bulb small, well developed. Caeca terminate at mid-body. Testes oblique, well anterior to ventral sucker. Ovary entire, distinctly posterior to and separate from testes. Vitelline follicles profuse, extend from oesophagus to testes. Excretory pore subterminal; excretory papilla absent. In intestine of marine teleosts (Acanthuridae only); East Pacific Ocean. Type- and only species *I. vogelsangi* Caballero & Bravo-Hollis, 1952.

1b. Ovary anterior to or between testes; body pyriform or elongate with pronounced dorsoventral curvature ..... 2.

2a. Oesophageal bulb absent ..... *Apharyngogyliauchen* Yamaguti, 1942. (Fig. 52.2)

Diagnosis: Body pyriform, dorsoventrally curved. Ventral sucker distinctly subterminal. Oesophagus almost straight. Oesophageal bulb absent. Caeca occupy approximately one third of total body-length, terminate in posterior third of body. Testes symmetrical, antero- or poster-

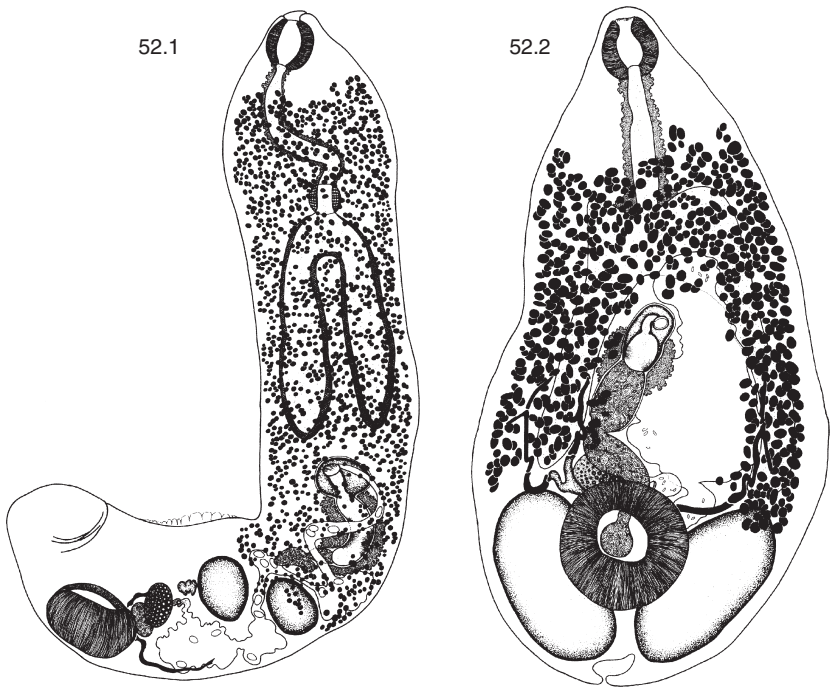


Fig. 52.1. *Ichthyotrema vogelsangi* Caballero & Bravo-Hollis, 1953. Paratype. From intestine of *Prionurus punctatus* (Acanthuridae), off Mexico. Original. Ventral sucker retracted in this specimen; in others, ventral sucker is not retracted and is at posterior extremity of body but, in these specimens, not all internal features are clearly visible.

Fig. 52.2. *Apharyngogyliauchen callyodontis* Yamaguti, 1942. Voucher. From intestine of *Hipposcarus harid* (Scaridae), Red Sea. Original.

olateral to ventral sucker. Ovary entire, anterior to or between testes. Vitelline follicles profuse, extend from level of pharynx or oesophagus to anterior margin of testes. Excretory pore terminal; excretory papilla absent. In intestine of marine teleosts (exclusively Scaridae and Labridae); Indo-Pacific region. Type-species *A. callyodontis* Yamaguti, 1942.

2b. Oesophageal bulb present ..... 3.

3a. Body extremely slender, narrowest in posterior third of body, conforms to contour of gonads; tegument of at least posterior third of body with prominent annulation .... *Affecauda* Hall & Chambers, 1999. (Figs 52.3, 52.4)

Diagnosis: Body elongate, narrowest in posterior third of body, strongly dorsoventrally curved; tegument annulated. Ventral sucker at posterior extremity. Oesophagus sigmoid or forms one loop. Oesophageal bulb present. Caeca terminate in anterior half of body. Testes tandem. Ovary entire, between testes. Vitelline follicles profuse, dense, surround oesophagus and caeca. Excretory pore distinctly dorso-subterminal; excretory papilla distinct. In intestine of marine teleosts (exclusively Acanthuridae); Indo-Pacific region. Type- and only species *A. annulata* Hall & Chambers, 1999.

3b. Body widest in posterior third of body; tegument without prominent annulation ... . 4.

4a. Oesophageal bulb weakly developed .... *Leptobulbus* Manter & Pritchard, 1962. (Fig. 52.5)

Diagnosis: Body pyriform. Ventral sucker in posterior half of body but distinctly separated from posterior extremity. Oesophagus almost straight. Oesophageal bulb weakly developed. Caeca terminate dorsal to ventral sucker. Testes symmetrical, posterolateral to ventral sucker. Ovary entire, posterior to and between testes. Vitelline follicles profuse, extend from level of oesophagus to anterior margin of testes. Excretory pore terminal; excretory papilla absent. In intestine of marine teleosts (exclusively Scaridae and Pomacanthidae); Indo-Pacific region. Type- and only species *L. magnacirratus* Manter & Pritchard, 1962.

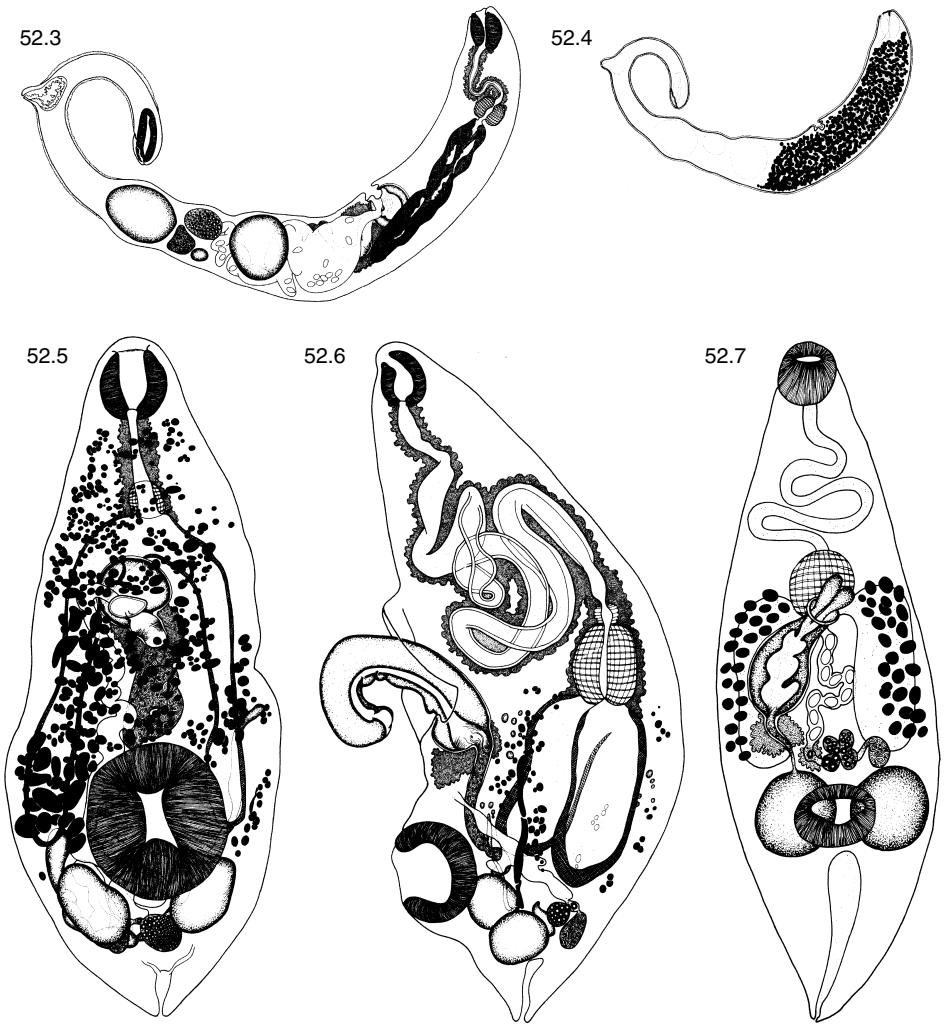
4b. Oesophageal bulb well developed ..... 5.

5a. Oesophagus length > 55% of body-length ..... 6.
5b. Oesophagus length < 50% of body-length ..... 7.

6a. Ovary entire ..... *Gyliauchen* Nicoll, 1915. (Fig. 52.6)
(Syn. *Dissotrema* Goto & Matsudaira, 1918)

Diagnosis: Body elongate to pyriform. Ventral sucker close to posterior extremity. Oesophagus with single loop or highly convoluted, at least 55% of body-length, often > 90%. Oesophageal bulb present, large. Caeca terminate from mid-body to level of testes. Testes tandem, oblique or symmetrical. Ovary entire, between or anterior to testes. Vitelline follicles profuse; distribution variable, but always follows at least length of caeca and terminates anteriorly to level of ventral sucker. Excretory pore distinctly dorso-subterminal; excretory papilla often distinct. In intestine of marine teleosts (predominantly Siganidae and Zanclidae); Indo-Pacific region. Type-species *G. tarachodes* Nicoll, 1915.

6b. Ovary four-lobed ..... *Progyliauchen* Shalaby & Hassanine, 1997 (Fig. 52.7)



Figs 52.3, 52.4. *Affecauda annulata* Hall & Chambers, 1999. Voucher. From intestine of *Naso tuberosus* (Acanthuridae), off Queensland, Australia. After Hall & Chambers (1999).
Fig. 52.5. *Leptobulbus magnacirratus* Manter & Pritchard, 1962. Paratype. From intestine of *Scarus* sp. (Scaridae), off Hawaii. Original.
Fig. 52.6. *Gyliauchen nahaensis* Ozaki, 1937. Voucher. From intestine of *Siganus punctatus* (Siganidae), location unknown. Original.
Fig. 52.7. *Progyliauchen sigani* Shalaby & Hassanine, 1997. From *Siganus rivulatus* (Siganidae), Red Sea. After Shalaby & Hassanine (1997a). Shalaby & Hassanine (1997) did not show gland-cells surrounding the oesophagus in their 'schematic' figure, so none are shown here, but dense gland-cells probably surround the oesophagus.

Diagnosis: Body elongate to pyriform. Ventral sucker in posterior third of body, well separated from posterior extremity. Oesophagus convoluted into lateral folds, > 55% total body-length. Oesophageal bulb present, large. Caeca occupy middle third of body. Testes symmetrical, dorsal to ventral sucker. Ovary four-lobed, anterior to and between testes. Vitelline follicles profuse,

surround caeca only. Excretory pore distinctly dorso-subterminal. In intestine of marine teleosts (Siganidae only); Indo-Pacific region. Type- and only species *P. sigani* Shalaby & Hassanine, 1997.

7a. Excretory papilla distinct; excretory pore distinctly dorso-subterminal ..... 8.
7b. Excretory papilla absent; excretory pore terminal ..... 9.

8a. Ventral sucker conspicuously elongate; excretory papilla enormous; testes posterior to ventral sucker ..... *Telotrema* Ozaki, 1933. (Fig. 52.8)
Diagnosis: Body elongate. Ventral sucker conspicuously elongate, ventro-subterminal. Oesophagus sigmoid, rarely straight, < 50% body-length. Oesophageal bulb present. Caeca terminate near mid-body. Testes tandem, posterior to ventral sucker; posterior testis distinctly elongate and may partly enter excretory papilla. Ovary entire, anterior to testes. Vitelline follicles profuse, surround oesophagus and caeca. Excretory pore distinctly dorso-subterminal; excretory papilla enormous. In intestine of marine teleosts (exclusively Acanthuridae); Indo-Pacific region. Type-species *T. caudatum* Ozaki, 1933.

8b. Ventral sucker nearly spherical, excretory papilla small; testes anterior to ventral sucker ..... *Flagellotrema* Ozaki, 1936. (Fig. 52.9)
Diagnosis: Body elongate. Ventral sucker, nearly spherical, close to posterior extremity. Oesophagus convoluted, < 50% of body-length. Oesophageal bulb present. Caeca terminate in mid-body. Testes oblique, anterior to ventral sucker. Ovary entire, between testes. Vitelline follicles profuse, surround oesophagus and caeca and extend to level of testes. Excretory pore distinctly dorso-subterminal; excretory papilla small, but distinct. In intestine of marine teleosts (exclusively Acanthuridae); Indo-Pacific region. Type-species *F. convolutum* Ozaki, 1936.

9a. Ventral sucker distinctly separated from posterior end of body; testes largely or entirely posterior to ventral sucker ..... *Paragyliauchen* Yamaguti, 1934. (Fig. 52.10)
Diagnosis: Body pyriform. Ventral sucker distinctly separated from posterior end of body. Oesophagus almost straight, only slightly sigmoid. Oesophageal bulb present. Caeca terminate at level of ventral sucker. Testes symmetrical, largely or entirely posterior to ventral sucker, at posterior end of body. Ovary entire, anterior to or between testes. Vitelline follicles profuse, along caeca. Excretory pore dorso-subterminal; excretory papilla absent. In intestine of marine teleosts (Pomacanthidae, Chaetodontidae and rarely Blenniidae); Indo-Pacific region. Type-species *P. chaetodontis* Yamaguti, 1934.

9b. Ventral sucker close to posterior end of body; testes largely or entirely anterior to ventral sucker ..... *Hadrobolbus* n. g. (Fig. 52.11)
Diagnosis: Body elongate to pyriform. Tegument smooth. Oral sucker absent. Ventral sucker at posterior extremity, round, larger than pharynx. Prepharynx absent. Pharynx surrounds mouth, subterminal, pyriform. Oesophagus sigmoid or forms single loop; straightened length less than quarter of body-length. Oesophageal bulb massive, frequently wider than long. Intestinal bifurcation immediately posterior to oesophageal bulb, at junction of anterior and second third of body. Caeca blind, short, terminate close to gonads. Testes two, symmetrical, globular, largely or entirely anterior to ventral sucker. Seminal vesicle large, tubular, bipartite, partly external to cirrus-sac, opens into prominent pars prostatica within cirrus-sac. Pars prostatica fed by profuse glands, external to cirrus-sac, which penetrate cirrus-sac wall. Cirrus-sac well developed, enclosing large, wide ejaculatory duct; ejaculatory duct sometimes with ridge-like cuticular markings. Genital atrium prominent. Genital pore median. Ovary entire, posterior to or

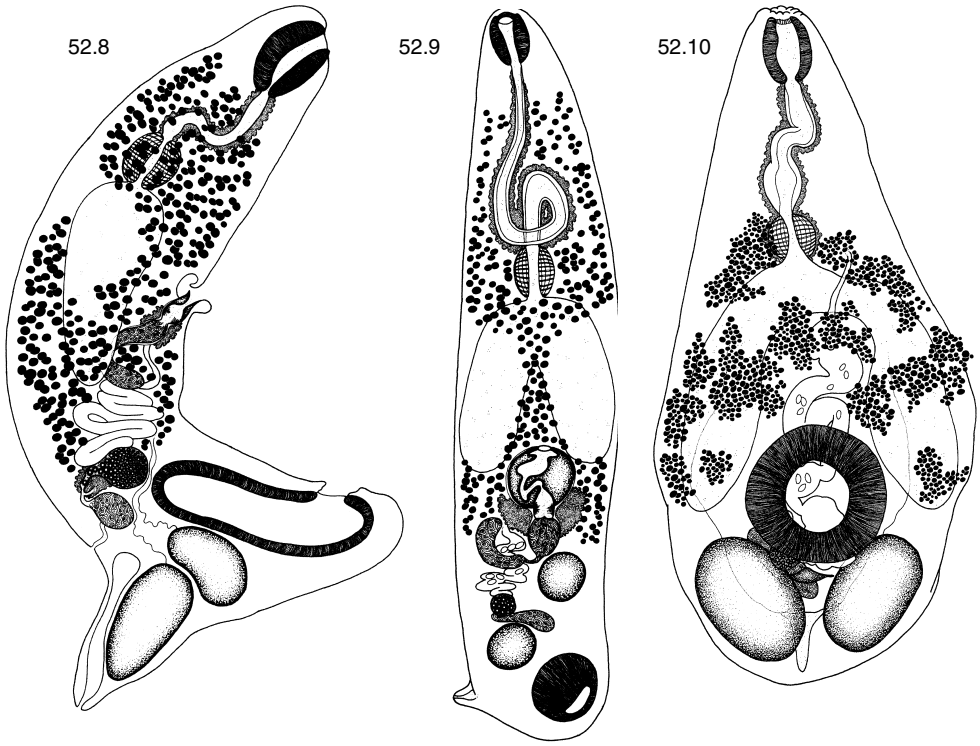


Fig. 52.8. *Telotrema caudatum* Ozaki, 1933. From intestine of *Prionurus scalprus* (Acanthuridae), off Japan. After Ozaki (1937b).
Fig. 52.9. *Flagellotrema convolutum* Ozaki, 1936. From intestine of *Prionurus scalprus* (Acanthuridae), off Japan. After Ozaki (1936b).
Fig. 52.10. *Paragyliauchen chaetodontis* Yamaguti, 1934. Holotype. From intestine of *Chaetodon* sp. (Chaetodontidae), off Japan. Original.

between testes. Mehlis' gland well developed. Canalicular seminal receptacle present, associated with insemination chamber. Laurer's canal present, opens posterodorsally to egg-forming complex. Uterus passes anteriorly from ovary. Eggs yellow, operculate, 50–80 μm long. Vitellarium follicular, scant, along oesophagus and caeca. Excretory vesicle I-shaped; collecting ducts arise anterolaterally, frequently observed along entire length, commencing at level of pharynx; excretory papilla absent; pore terminal. In intestine of marine teleosts (exclusively Acanthuridae, Chaetodontidae and Pomacanthidae); Indo-Pacific region. Type-species *H. chaetodontis* (Manter & Pritchard, 1962) n. comb.

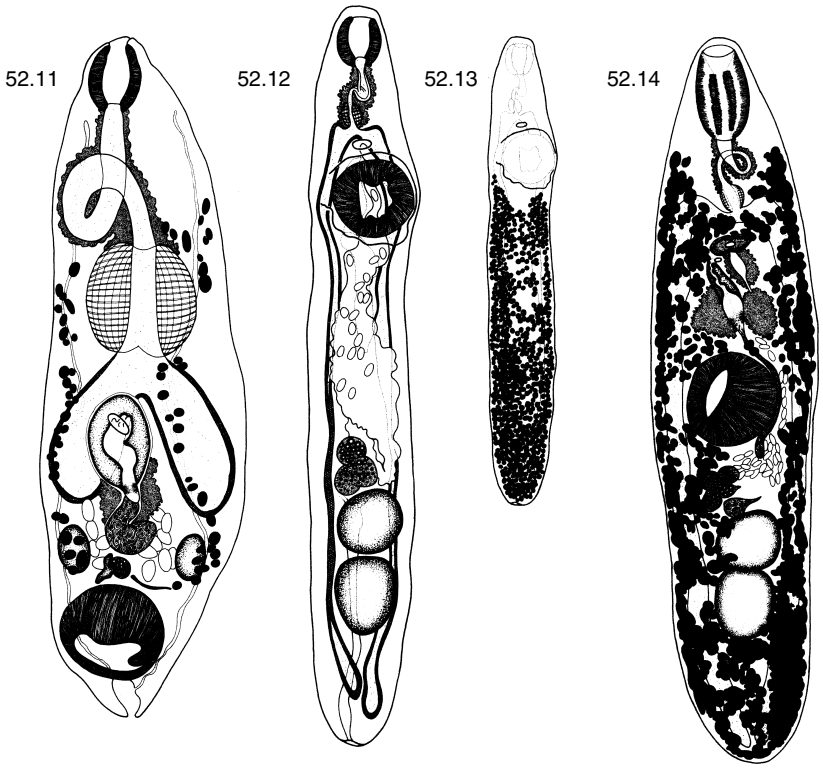


Fig. 52.11. *Hadrobolbus centropygis* (Yamaguti, 1970) n. comb. Holotype. From intestine of *Centropyge potteri* (Pomacanthidae), off Hawaii. Original. AQ1
Figs 52.12, 52.13. *Petalocotyle diverticulata* Hall & Cribb, 2000. From intestine of *Acanthurus nigrofuscus* (Acanthuridae), off Queensland, Australia. After Hall & Cribb (2000).
Fig. 52.14. *Robphildollfusium fractum* Paggi & Orecchia, 1963. From *Sarpa salpa* (Sparidae), Mediterranean Sea. After Bartoli (1987).

Author Query

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